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Sterling J. Nesbitt[1*], Robert K. Denton Jr.[2], Mark A. Loewen[3], Stephen L. Brusatte[4], Nathan D. Smith[5], Alan H. Turner[6], James I. Kirkland[7], Andrew T. McDonald[8], and Douglas G. Wolfe[9]

[1]Department of Geosciences, Virginia Tech, Blacksburg, Virginia 24061, USA. [2]GeoConcepts Engineering, a Terracon Company, Ashburn, Virginia 20147, USA. [3]Natural History Museum of Utah and Department of Geology & Geophysics, University of Utah, Salt Lake City, Utah 84108, USA. [4]School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FE, UK. [5]Dinosaur Institute, Natural History Museum of Los Angeles County, Los Angeles, California 90007, USA. [6]Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York, 11794, USA. [7]Utah Geological Survey, P.O. Box 146100, Salt Lake City, Utah 84114, USA. [8]Western Science Center, Hemet, California 92543 USA. [9]Zuni Dinosaur Institute for Geosciences, Springerville, Arizona 85938 USA.

**Contact*: sjn2104@vt.edu

Late Cretaceous dinosaur assemblages of North America – characterized by gigantic tyrannosaurid predators and large-bodied herbivorous ceratopsids and hadrosaurids - were highly successful from ca. 80 Ma until the end of the 'Age of Dinosaurs' 66 Ma. However, the origin of these iconic faunas remains poorly understood because of a large, global sampling gap in the mid-Cretaceous, associated with an extreme sea-level rise. We describe the most complete skeleton of a predatory dinosaur from this gap which belongs to a new tyrannosauroid theropod from the Middle Turonian (~92 Ma) of southern Laramidia (western North America). This taxon, *Suskityrannus hazelae* gen. et sp. nov., is a small-bodied species phylogenetically intermediate between the oldest, smallest tyrannosauroids and the gigantic, last-surviving tyrannosaurids. The species already possesses many key features of the tyrannosaurid bauplan, including the phylogenetically earliest record of an arctometatarsalian foot in tyrannosauroids, indicating that group developed enhanced cursorial abilities at small body size. *Suskityrannus* is part of a transitional Moreno Hill (=Zuni) dinosaur assemblage that includes dinosaur groups that become rare or are completely absent in North America and small-bodied forebears of the large-bodied clades that dominated the final ca. 15 million years of the North American Cretaceous before the end-Cretaceous mass extinction.

During the latest Cretaceous, the former continent of Laramidia—today's western North America—was populated by an iconic assemblage of dinosaurs. This assemblage includes tyrannosaurids like *Tyrannosaurus rex* and a variety of herbivores, among them horned

ceratopsids (*Triceratops* and kin), duck-billed hadrosaurids, and armored ankylosaurs. These keystone groups formed some of the best-known dinosaur faunas of all, represented by an extensive fossil record stretching from the Arctic Circle to Mexico and spanning the final ca. 15 million years of the Cretaceous (ca. 80-66 Ma)[1,2]. It is clear that these 'last dinosaur faunas' met their demise suddenly, in the aftermath of the Chicxulub bolide impact and other global changes 66 million years ago[3,4]. What is largely unclear is how these communities were established, because the preceding ~20 million years of the mid-Cretaceous (ca. 100-80 Ma) are a dark interval of poor fossil preservation, seemingly the result of severe sea-level rise and other environmental changes[5-7]. During this gap, tyrannosauroids switched from small, gracile hunters to megapredators, and the classic latest Cretaceous herbivores increased in body size and ecological abundance. The nature of this transition, however, is hazy, as thus far it has been reconstructed from a patchwork of fragmentary fossils from geographically disparate localities in North America and Asia[8-10].

In recent years, the Zuni Basin of New Mexico, USA, has emerged as critical to our understanding the mid-Cretaceous evolution of dinosaurs[11-13]. The Turonian (ca. 92 Ma) Moreno Hill Formation has yielded a diversity of herbivorous species that provide a glimpse at the early evolution of key Late Cretaceous groups like ceratopsids, hadrosauroids, and therizinosaurids. We here describe a new species of tyrannosauroid from the Zuni Basin, based on two associated skeletons that represent the most complete specimens of a mid-Cretaceous tyrannosauroid yet known. This new species is phylogenetically intermediate between the grade of early-diverging, small to medium-sized tyrannosauroids that originated in the Middle Jurassic and the enormous, bone-crunching apex predator tyrannosaurids of the final ~20 million years of the Cretaceous. The new species demonstrates that several integral components of the tyrannosaurid-style body

plan, including a cursorially-adapted arctometatarsalian foot, evolved at small or medium body size. Finally, the new species is part of what we recognize here as the Moreno Hill Assemblage: small-bodied antecedents of the signature latest Cretaceous clades that formed the stock from which the last-surviving North American dinosaur communities were forged.

Results

Systematic Paleontology.

Dinosauria Owen, 1842 sensu[14]

Theropoda Marsh, 1881 sensu[15]

Coelurosauria[16] sensu[17]

Tyrannosauroidea[18] sensu[19]

Suskityrannus hazelae gen. et sp. nov.

Etymology. From the Zuni 'Suski' (coyote) and from Latin 'tyrannus' (king). The specific name is for Hazel Wolfe, whose tireless efforts, support, and sacrifices made possible much of the success at the Moreno Hill fossil localities.

Holotype. Arizona Museum of Natural History, Mesa, Arizona (MSM) P4754, partially articulated skull including part of premaxillae, maxillae, dentaries, palatines, vomers and jugals, partial splenials (Fig. 1), fragments of the braincase and parietal, and right articular and articulated quadrate (Fig. 1g, h). Postcrania includes two cervical vertebrae with cervical rib fragments (Fig. 2c, d), a trunk centrum, part of a sacral centrum, and distal portions of left metatarsals II-IV (Fig. 2u) and other fragments.

Paratype. MSM P6178, partially articulated and associated skeleton (Fig. 2) including: anterior portion of right dentary, left frontal, partial left postorbital, cervical, trunk, partial sacral, and

caudal vertebrae, isolated neural arches, partial left scapula, manual ungual fragments, partial pubes, femora, tibiae, fibulae, astragali, partial right pes, and bone fragments. The referred specimen was found 30 meters away from the holotype specimen at the same horizon and is nearly identical in size. The morphology is identical where the two specimens overlap (dentary, cervical and trunk vertebrae, and pes) and the referred specimen possesses tyrannosauroid character states (see below).

Locality and age. Mirror Mesa locality (MSM locality 98-67; on file at MSM), lower member of the Moreno Hill Formation, Zuni Basin, New Mexico (see supplementary information). The age of the Moreno Hill Formation is considered early Middle Turonian (~ 92 Ma) based on ammonite biostratigraphy in strata that interfinger with the formation[13,20].

Diagnosis. Tyrannosauroid theropod with the following autapomorphies among tyrannosauroids: 1) distal condyles of femur strongly mediolaterally compressed with crista tibiofibularis that merges smoothly into the lateral condyle laterally (in *Guanlong*, *Dilong*, *Juratyrant*, *Xiongguanlong*, *Dryptosaurus*, *Appalachiosaurus*, and tyrannosaurids the distal condyles are more bulbous and wider mediolaterally, and where well preserved, the crista tibiofibularis is offset from the lateral edge of the lateral condyle by a notch); 2) medial condyle of proximal end of tibia hooked posteromedially (in *Guanlong*, *Juratyrant*, *Xiongguanlong*, *Eotyrannus*, *Dryptosaurus*, *Appalachiosaurus*, and tyrannosaurids the medial condyle projects straight posteriorly).

As both autapomorphies are present on the paratype specimen only, we also note that the holotype of *Suskityrannus hazelae* can be distinguished from all other coelurosaurs, including other tyrannosauroids, by a unique combination of characters: D-shaped, incisiform, and carinate premaxillary teeth; anteroposteriorly shortened premaxilla (less than 10% anteroposterior length

of maxilla); maxilla main body maintaining constant depth across its length; surangular with dorsoventrally thick lateral shelf and small foramen; cervical vertebrae neural arches X-shaped in dorsal view with anteroposteriorly short neural spine; arctometatarsalian pes (see Supplemental Information for Differential Diagnosis).

Ontogenetic age and body size. To estimate the ontogenetic age of the specimens of *Suskityrannus*, we evaluated a combination of skeletal maturity indicators and histological methods, as typically used for dinosaurs[21]. The holotype and the referred specimen are approximately the same size, so we treat them together here. The neural arches and centra are fused in the cervical, anterior trunk, and mid-to-distal caudal vertebrae, but are unfused (and found disarticulated from each other) in the posterior trunk, sacral, and anterior caudal vertebrae. Although the sequence of neurocentral suture closure is not clear in many dinosaur groups[22], the lack of fusion in part of the sequence in an archosaur suggest skeletal immaturity[23]. A histological section from the mid-shaft of the femur (Fig. 3) exhibits a minimum of three widely-spaced growth lines with no sign of decreasing growth rate (e.g., similar tissues throughout the cortex, no secondary osteons), indicating that the individual was young and actively growing at the time of death. A similarly small number of growth lines are observed in young specimens[24,25] of large-bodied tyrannosaurids. However, and critically, the bone tissues and vascularization (longitudinal, reticular and occasional circumferential) of *Suskityrannus* differ from these young tyrannosaurids, which possess sub-plexiform vascular organization. This suggests that *Suskityrannus*: 1) grew like smaller theropods with femoral length between 10 – 30 cm[26] and did not reach the mature size of tyrannosaurids and; 2) grew much more slowly than tyrannosaurids and more like earlier tyrannosauroids (e.g., *Guanlong*[27]). Although it is difficult to estimate the skeletally mature or adult body size of *Suskityrannus*, it was most likely much smaller than the

majority of Campanian-Maastrichtian tyrannosaurids given our current knowledge of dinosaur growth and the histological and skeletal features of the two specimens of *Suskityrannus* (see supplementary information).

Comparative Description.

The skull is small, estimated at ~25-32 cm in total length (based on other tyrannosauroids [28,29]), and has a long and low snout in lateral view. The snout is broadly U-shaped anteriorly, such that all four premaxillary teeth are oriented mediolaterally, a feature of *Xiongguanlong* and Late Cretaceous tyrannosauroids that is unique among coelurosaurs[30]. The premaxilla is short, and measures less than 10% of the anteroposterior length of the maxilla, as in all tyrannosauroids and a few other coelurosaurs[31]. The maxilla is long and low, as in early-diverging tyrannosauroids and *Xiongguanlong*, not dorsoventrally deep as in large tyrannosaurids and *Yutyrannus*[32]. The bone has a straight ventral margin, as in early tyrannosauroids and most other coelurosaurs, but unlike the ventrally convex profile of *Xiongguanlong*, *Timurlengia*, and Late Cretaceous tyrannosauroids[17,30]. The main body of the maxilla maintains a relatively constant depth for most of its length, also the case in early tyrannosauroids and *Xiongguanlong*, but unlike the tapering condition of *Timurlengia* and younger taxa[33]. An extensive antorbital fossa covers much of the lateral surface of the maxilla and bears an enlarged maxillary fenestra and a small promaxillary fenestra, which is largely obscured by damage.

The frontal is elongate anteroposteriorly, having a length-to-width ratio greater than 2.0, and makes a wide contribution to the orbital rim. Both conditions are shared with *Guanlong* and *Dilong*, but are absent in later-diverging taxa, which have shortened frontals with a small, notch-like (or absent) orbital rim[17,30,33]. Other portions of the cranium are extremely fragmentary. The postorbital bears small lineations on the orbital margin (similar to immature specimens of

Alioramus[34]), the palatine has a pneumatic recess ventral to the vomeropterygoid process, and the braincase appears to possess a deep and well-defined otic recess as in *Timurlengia*[35] and a large posterior tympanic recess.

The robust dentaries taper anteriorly and lack the anteroventral inflection point ('chin') of tyrannosaurids. Part of a dorsoventrally deep shelf is on the lateral surface of the surangular, a feature of *Eotyrannus* and later-diverging tyrannosauroids, unlike the thinner (or absent) shelves of other theropods[17,30,33]. The posterior surangular foramen is present, unlike in early tyrannosauroids like *Guanlong* and *Dilong*, but is not expanded into a window-like opening as in *Dryptosaurus* and tyrannosaurids[17,30,31]. The retroarticular process is highly reduced, a key synapomorphy of tyrannosauroids[31] and has the tyrannosaurid-style conditions of a wide muscle attachment site and lack of a non-articular region between the muscle attachment and glenoid[33,36].

The premaxilla bears four teeth, which are considerably smaller than the maxillary teeth and have straight posterior margins and D-shaped cross sections, all features of tyrannosauroids[31,33]. CT data reveal 13 teeth on the maxilla, which are recurved and finely serrated (4.5/mm) on both mesial and distal carinae. The dentary has 16 teeth, the first two of which are smaller than the anterior premaxillary teeth.

The anteroposteriorly short cervical vertebrae (Fig. 2c,d) are weakly opisthocoelous with anteroposteriorly short neural spines that impart an X-shape to the neural arch in dorsal view. This latter condition is present in tyrannosaurids, but contrasts with the longer, more sheet-like neural spines in *Xiongguanlong* and earlier tyrannosauroids[33]. One large pneumatic foramen (= pleurocoel) is present on the anterior region of the lateral surface of the centrum which is bordered dorsally by a nearly horizontal posterior centrodiapophyseal lamina, a rare morphology

also present in the tyrannosauroids *Guanlong*, *Dilong*, and *Eotyrannus* but differing from the posteroventrally inclined lamina of tyrannosaurids and most other theropods[33]. All known trunk vertebrae are not as strongly spool-shaped as in *Xiongguanlong* and later tyrannosauroids, and have a pneumatic foramen on the anterior half. The caudal vertebrae are unremarkable for theropods.

The incomplete scapula has a posterolaterally directed glenoid, but, other than incomplete manual unguals, the remainder of the forelimb is unknown. The anterior edge of the pubic shaft is concave in lateral view as in *Dryptosaurus*, *Appalachiosaurus*, and tyrannosaurids, and not straight as in *Guanlong* and *Dilong*[30]. The femur has a dorsally inclined head, characteristic of most tyrannosauroids[31,33] and some other large theropod clades (e.g., carcharodontosaurids), and has an alariform anterior (=lesser) trochanter bearing an accessory trochanter, features of early tyrannosauroids and *Xiongguanlong* that contrast with the reduced trochanter of tyrannosaurids[31,33]. The extensor groove on the distal end of the femur is shallowly excavated, intermediate between the flat anterior surface of *Guanlong* and *Dilong* and the deeply impressed, U-shaped clefts of *Xiongguanlong* and Late Cretaceous tyrannosauroids[33]. The tibia is estimated to be longer than the femur (supplemental information), the fibula narrows distally to a splint, and the astragalus has a proximally elongated, sheet-like ascending process. The most salient feature of the hindlimb is the arctometatarsalian metatarsus, with metatarsal III pinched between metatarsals II and IV proximally, essentially identical to the classic tyrannosaurid condition[37], albeit at smaller size. The pes of *Suskityrannu*s clearly differs from the non-arctometatarsalian pes of early tyrannosauroids (*Yutyrannus*[32], *Guanlong*, *Dilong*, *Kileskus*, *Eotyrannus*[33]). The tyrannosaurid condition is also present in the large-bodied, non-tyrannosaurids *Appalachiosaurus* and *Dryptosaurus*, but unfortunately the metatarsus is unknown in key transitional taxa (e.g.,

Xiongguanlong and *Timurlengia*).

Phylogenetic position. To test the phylogenetic position of *Suskityrannus*, we employed three phylogenetic datasets to 1) establish the relationship of the new taxon within a broad context of theropod relationships and 2) establish its position within Tyrannosauroidea, accounting for variation/discrepancy in two recent and partially independent datasets. First, we scored the new taxon into the Theropod Working Group dataset[31,35], which includes a wide sample of coelurosaurs and outgroups scored for over 850 discrete anatomical characters. The result was the recovery of 10,000+ most parsimonious trees (length = 3774, Consistency Index = 0.321, Retention Index = 0.778; supplementary information). The strict consensus places *Suskityrannus* in the same region of the phylogeny as *Xiongguanlong* and *Timurlengia*: intermediate between the mostly small-bodied, early-diverging taxa (*Guanlong* and other proceratosaurids, *Dilong*, *Eotyrannus*, *Juratyrant*) but outside of the clade of large-bodied tyrannosaurids and immediate outgroups. The tyrannosauroid affinities of *Suskityrannus* are substantiated by comparatively high tree support values and numerous unambiguous synapomorphies of Tyrannosauroidea or less inclusive clades, including a U-shaped snout, a prominent surangular shelf, an extremely reduced retroarticular process, straight premaxillary teeth, and a dorsally inclined femoral head.

With the tyrannosauroid affinities of *Suskityrannus* established, we then added it to two tyrannosauroid-specific datasets[38,39] which included a larger sampling of tyrannosauroids than in the first analysis. The first dataset[38] resulted in the recovery of five most parsimonious trees (length = 766, Consistency Index = 0.555, Retention Index = 0.813; supplementary information), the strict consensus of which places *Suskityrannus* in an identical 'intermediate' phylogenetic position as the Theropod Working Group analysis whereas the second independent

tyrannosauroid-specific dataset[39] resulted in the recovery of two most parsimonious trees (length = 1894, Consistency Index = 0.352, Retention Index = 0.753; supplementary information) where *Suskityrannus* was found closer to but still outside of Tyrannosauridae. Both tyrannosauroid-specific datasets[38,39] differ in optimizations of character states, the inclusion of taxa and characters; nevertheless, all three analyses place *Suskityrannus* outside of Tyrannosauridae as an 'intermediate' tyrannosauroid (Fig. 4a).

Discussion

The discovery of *Suskityrannus* helps fill major phylogenetic, morphological, and temporal gaps in tyrannosauroid evolution (Fig. 4a), and in doing so clarifies how these dinosaurs transitioned from small, gracile species into enormous apex predators that characterized the last-surviving dinosaur faunas of Laurasia.

Tyrannosauroids were a geographically widespread group of mostly small-bodied (human-to-horse-size) species during the Middle Jurassic-Early Cretaceous[27,29,40], and then in the latest Cretaceous (Campanian-Maastrichtian) became restricted to Asia and North America; in western North America (Laramidia) they developed into multi-ton, bone-crunching carnivores as exemplified by *Tyrannosaurus rex*[33]. This dramatic switch occurred sometime in the mid-Cretaceous, a ca. 20 million year span between the end of the Albian to the early Campanian, that witnessed extensive environmental change including ocean anoxia, temperature increase, and a global ocean transgression[5,7]. Very few dinosaur fossils are known from this time, probably the result of the high sea levels that flooded the continents and decreased preservation potential[5]. Previously, only a single diagnostic tyrannosauroid had been described from this mid-Cretaceous gap (Fig. 4a): *Timurlengia euotica* from the Bissekty Formation of Uzbekistan[35], represented

only by a braincase and a constellation of isolated bones from many individuals. *Suskityrannus*, however, is represented by two associated and partially articulated skeletons which contain key portions of the anatomy unknown in *Timurlengia*, particularly the hindlimb. Thus, *Suskityrannus* provides our best glimpse yet at a mid-Cretaceous tyrannosauroid.

Our phylogenetic analysis recovers *Suskityrannus* as an intermediate tyrannosauroid nested between the smallest, earliest-diverging species from the Middle Jurassic–Early Cretaceous and the giants of the latest Cretaceous. Also included in this intermediate zone are the mid-Cretaceous *Timurlengia* and *Xiongguanlong* – an Asian taxon that lived immediately prior to the mid-Cretaceous gap[41]. These species form a ladderized grade instead of a clade suggesting that transitional tyrannosauroids were widely distributed across the unflooded northern continents during the mid-Cretaceous. Although the adult sizes of any of these species are uncertain, they were clearly much smaller than the latest Cretaceous tyrannosaurids. Nevertheless, as previously recognized in *Timurlengia* and *Xiongguanlong*, they already possess several components of the so-called 'tyrannosaurid bauplan': features related to increased bite forces and neurosensory abilities that were later integral to the ecological dominance of *T. rex* and kin[35,38]. *Suskityrannus* corroborates this finding, as it also possesses tyrannosaurid-style cranial features such as a U-shaped snout. *Suskityrannus* demonstrates that the tyrannosaurid-style arctometatarsalian foot was also present in intermediate-grade, small-bodied species (Fig. 4a). An arctometatarsalian metatarsus evolved independently in at least three theropod clades and is associated with enhanced cursorial abilities[37]. The absence of an arctometatarsalian pes in the otherwise gracile, long-limbed, and likely cursorial early tyrannosauroids like *Dilong* and *Guanlong* is notable and may suggest that tyrannosaurids evolved a pinched metatarsus to retain (or improve) cursorial locomotion at gigantic body size. *Suskityrannus* presents the earliest

record of this signature feature in a tyrannosauroid, both phylogenetically and temporally, and indicates that it developed prior to the evolution of large size. Thus, many of the most noteworthy components of the tyrannosaurid body plan—a robust skull that could bite strongly, a large brain and keen senses, and a cursorial foot—evolved in mid-sized species that lived long before tyrannosaurids assumed ecological dominance. It is unclear why these animals were drastically changing so many aspects of their anatomy and biology during the mid-Cretaceous. This may have been related to some of the environmental changes occurring during this time, although the sparse fossil record makes that difficult to test. Alternatively, these developments may have been adaptations for hunting at medium size, in ecosystems where late-surviving allosauroids remained incumbent in the top predator niche earlier in the Cretaceous[42].

Not only does *Suskityrannus* fill an important gap in tyrannosauroid evolutionary history, it is also part of a critically important dinosaur assemblage—the Moreno Hill (=Zuni) Assemblage—that illuminates the transition between Early Cretaceous faunas and the classic, well-studied latest Cretaceous dinosaur ecosystems (Fig. 4b-d). Turonian-age dinosaur assemblages are extremely rare worldwide[5] and particularly in North America and Asia, where the record consists merely of rare trackways (e.g., Kaskapau Formation[43]), isolated bones (Bissekty Formation[8]), microvertebrate assemblages (Straight Cliffs Formation[44]), or a combination of these (Straight Cliffs Formation[44]) . These records give information on the presence or absence of broad dinosaur groups but their incompleteness limits taxonomic and phylogenetic precision. The Moreno Hill Assemblage, on the other hand, now boasts several dinosaurs represented by partial skeletons which can be placed in a phylogenetic context. These include the new tyrannosauroid *Suskityrannus*, the neoceratopsian *Zuniceratops christopheri*[13],

the hadrosauromorph *Jeyawati rugoculus*[12], the therizinosaurid *Nothronychus mckinleyi*[11] and ankylosaur fossils (see supplemental information).

The Moreno Hill Assemblage provides several key insights. First, the main members of the assemblage—*Suskityrannus*, *Zuniceratops*, *Jeyawati*—clearly are phylogenetically positioned just outside the major Late Cretaceous radiations of tyrannosaurids, ceratopsids, and hadrosaurids, respectively. Additionally, these animals are all smaller than later-diverging members of their clades present in the next dinosaur-rich western North American formation, the Wahweap Formation (ca. 80 million years old) and in subsequent formations until the end-Cretaceous. They appear, therefore, to be early diverging, small-bodied representatives of the groups that would eventually diversify into the key ecological players of latest Cretaceous North America. On the other hand, the Moreno Hill Assemblage does contain a therizinosauroid (*Nothronychus*), a group common in the Early Cretaceous but apparently absent or restricted to poorly sampled ecosystems in the latest Cretaceous of most of North America (exceptions are therizinosauroid tracks in the unusual high-latitude faunas of Alaska[45] and other possible tracks from Colorado[46]). Finally, although sampling biases may confound this observation, the Moreno Hill Assemblage is also notable for what it lacks: sauropods, allosauroids, and iguanodontian-grade ornithopods, groups that are common and diverse in the Early Cretaceous of North America but absent or geographically restricted in the latest Cretaceous.

Thus, the Moreno Hill Assemblage captures the transition from the Early Cretaceous to the latest Cretaceous, with a combination of dinosaur clades that become rare or extirpated and founder species that mark the beginning of the dinosaur dynasties of the Campanian-Maastrichtian of western North America. These mid-Cretaceous faunas, probably shaped by marine transgression and other environmental changes that are still difficult to decipher, gave

rise to the most iconic dinosaur faunas of all: the tyrannosaurid-ceratopsid-hadrosaurid communities that persisted until the end-Cretaceous asteroid impact 66 million years ago.

Methods

Histological preparation methods. The femoral fragment, taken near the broken surface, was removed using an IsoMet 4000 saw equipped with a diamond wafering blade, embedded in Castolite AP and vacuumed, and then cut into thin sections with an IsoMet 4000 saw equipped with a diamond wafering blade. Each section was ground with a 1200-grit grinding disc and then fixed on 2a 0.3-mm-thick plastic slide with Aron Alpha (Type 201) cyanoacrylate. The slides were then ground by hand through a cascading sequence of finer grits until final polishing. The slide was then imaged using a Nikon Eclipse LV100ND transmitted and reflected light microscope, imaging them using a Nikon DS-Fi2 camera and Digital sight DS-U3 interface together with a Prior ProScan III automated microscope stage and digitally assembled using Nikon NIS-Element Basic Research v. 4.40.00 (Build 1084). These full-slide images were captured in plane-polarized light and cross-polarized light with a gypsum plate (530 nm). Both high resolution sections are available on Morphobank (Project Number 3298; Permalink: http://morphobank.org/permalink/?P3298).

Computed tomographic methods. We CT scanned the anterior portion of the skull at Duke University's Shared Materials Instrumentation Facility using a Nikon XTH 225 CT high-resolution micro-CT scanner. The specimen is available to view or download on MorphoSource (www.morphosource.org). Scanning parameters include: 220 kV and 0.27 mA. The beam passed through 1-mm copper plate. Data was visualized in Mimics 20.0 to observe morphology within the specimen.

Phylogenetic methods. To assess the phylogenetic relationships of *Suskityrannus hazelae* we added it to three phylogenetic datasets[31,38,39]. First, we added the taxon to the latest major iteration of the Theropod Working Group (TWiG) Dataset, a 20+ year research program that has been building progressively larger datasets of theropod phylogeny based on direct examination of specimens. We used the dataset of Brusatte et al.[35], which is a slightly modified version of Brusatte et al.[31]. We made one scoring change to this dataset: *Timurlengia* was changed from state ? to 1 for character 503. Our final dataset thus includes 154 taxa scored for 853 discrete anatomical characters, covering a broad diversity of coelurosaurs and outgroups. We analyzed the dataset in TNT v1.1[47] under maximum parsimony. Following previous TWiG protocols, we used the outgroup *Allosaurus* to root the tree. The following characters were ordered: 3, 16, 17, 18, 19, 24, 25, 27, 38, 39, 40, 45, 63, 66, 72, 74, 89, 103, 108, 111, 114, 117, 119, 121, 123, 130, 146, 148, 152, 154, 161, 163, 166, 168, 169, 171, 175, 178, 179, 181, 195, 197, 200, 217, 222, 232, 234, 235, 238, 242, 250, 252, 255, 256, 261, 262, 265, 268, 270, 279, 287, 292, 299, 309, 316, 319, 321, 326, 328, 347, 351, 359, 364, 379, 384, 385, 387, 393, 397, 401, 409, 413, 415, 417, 420, 425, 426, 427, 428, 433, 434, 443, 445, 446, 459, 462, 475, 482, 485, 488, 494, 499, 520, 540, 545, 556, 557, 560, 578, 579, 605, 613, 622, 628, 631, 632, 635, 642, 648, 651, 665, 669, 670, 684, 694, 698, 702, 711, 712, 715, 727, 728, 763, 780, 805, 806, 807, 818, 823, 842, 843. We first analyzed the data matrix under the "New Technology" search options, using sectorial search, ratchet, tree drift, and tree fuse options with default parameters. The minimum length tree (= most parsimonious tree, MPT) was set to run until the minimum length was hit 10 times; a procedure that samples as many tree islands as possible. The stored trees were then analysed under tree bisection and reconnection branch swapping, which aims to more fully

explore each tree island. Zero-length branches were collapsed following Rule 1 of Coddington and Scharff[48]. We constructed a strict consensus of MPTs by *a posterori* pruning five wildcard taxa: *Kinnareemimus*, *Epidendrosaurus*, *Pyroraptor*, *Hesperonychus*, and *Limenavis*.

As this first analysis with the TWiG dataset recovered *Suskityrannus* within Tyrannosauroidea, the second analysis focused more specifically on tyrannosauroid in-group relationships. We added *Suskityrannus* to the dataset of Brusatte and Carr[38] and made one scoring change (*Timurlengia* was changed from ? to 1 for character 35). Our final dataset thus includes 34 taxa scored for 366 characters. The following characters were ordered: 8, 9, 10, 13, 19, 23, 26, 31, 37, 38, 52, 72, 76, 81, 86, 94, 98, 99, 115, 119, 120, 158, 180, 181, 184, 191, 196, 198, 201, 217, 224, 239, 241, 257, 270, 278, 283, 285, 286, 290, 305, 323, 324, 333, 334, 343, 346. We analyzed it using the same protocols as above (including treating *Allosaurus* as the outgroup for tree rooting), the only difference being that 1,000 replicates were used for the jackknife analysis. We constructed a strict consensus of MPTs by *a posteriori* pruning one wildcard taxon identified by Brusatte and Carr[38]: *Aviatyrannis*.

The third phylogenetic dataset[39] also focused on tyrannosauroid in-group relationships. Several characters have been rescored for all taxa and many taxa have updated scorings. Several taxa were scored that were not present in the original dataset and some taxa are updated as new material has become available. The resultant dataset thus includes 57 taxa scored for 501 characters scored for all currently known tyrannosauroids. The following characters were ordered: 1, 2, 13, 39, 43, 46, 70, 94, 96, 100, 102, 108, 110, 126, 137, 147, 149, 152, 155, 160, 167, 177, 188, 200, 202, 207, 225, 269, 270, 272, 274, 276, 281, 291, 329, 351, 364, 406, 420, 425, 432, 442, 465, 470, 471, 489, 491. The dataset was analysed using TNT[47]. Tree searching followed the parsimony criterion implemented under the heuristic search option using tree

bisection and reconnection (TBR) with 10,000 random addition sequence replicates. Zero length branches were collapsed if they lacked support under any of the most parsimonious reconstructions.

Data availability. The data that support the findings of this study are in the supplemental data and high-quality images of the histology sections are available on Morphobank (Project Number 3298; Permalink: http://morphobank.org/permalink/?P3298). Reconstructed CT slices (.tiff stack format) are available for the holotype skull (MSM P4754) on http://www.morphosource.org/ doi:10.17602/M2/M68107. Data have been deposited in ZooBank under Life Science Identifier urn:lsid:zoobank.org:act:77D5BFA3-F936-4A91-B350-80DCEACB441C (for the new genus and species).

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Author contributions

S.J.N., R.K.D., M.A.L., and S.L.B. designed the research project; S.J.N. and A.H.T. composed the figures; S.L.B., and M.A.L. conducted the phylogenetic analyses; S.J.N., R.K.D., M.A.L., S.L.B, and N.D.S. interpreted the anatomy; D.G.W. R.K.D., and J.I.K. oversaw field work and

geological analysis; JIK oversaw preparation of specimens; S.J.N., R.K.D., M.A.L., S.L.B, N.D.S., A.H.T, J.I.K., A.T.M., and D.G.W. wrote the manuscript.

Competing interests

The authors declare no competing financial interests.

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Correspondence and requests for materials should be addressed to S.J.N.

FIGURE CAPTIONS

Figure 1 | *Suskityrannus hazelae*, gen. et sp. nov. holotype skull (a-h) (MSM P4754) and reconstruction (i). Anterior portion of the skull in right lateral (**a-b**), left lateral (**c**-**d**) and ventral (**e-f**) views. Right articular and partial surangular in lateral (**g**) and posterior (**h**) views. Reconstruction (**i)** of the skull based solely on the holotype. Red portions preserved in the holotype skull (partial braincase preserved, but not illustrated). Reconstruction based on other tyrannosauroid skulls. Abbreviations are as follows: anfe, antorbital fenestra; anfo, antorbital fossa; d, dentary; j, jugal; l., left; mx, maxilla; pal, mxf, maxillary fenestra; palatine pmx, premaxilla; qu, quadrate; r., right; rp, retroarticular process; suf, posterior surangular foramen. Reconstruction copyright Scott Hartman. Scale bars = 1 cm. **[planned for 1 column width]**

Figure 2 | Skeletal element of both specimens of *Suskityrannus hazelae*, gen. et sp. nov. (a-z) and reconstruction (center). Left frontal (MSM P6178) in dorsal (**a**) and lateral (**b**) views. **c**, Anterior portion of the dentary (MSM P6178) in lateral view. Middle cervical vertebra (MSM P4754) in left lateral (**d**) and ventral (**e**) views. Anterior trunk vertebra (MSM P6178) in left lateral (**f**) and posterior (**g**) views. **h**, Partial sacral centrum (MSM P6178) in dorsal view. **i**,

Posterior trunk centrum (MSM P6178) in right lateral view. **j**, Middle caudal vertebra (MSM P6178) in lateral view. **k**, Distal caudal vertebra (MSM P6178) in lateral view. Proximal half of the right femur (MSM P6178 in proximal (**l**) and posterior (**m**) views. Distal half of the right femur (MSM P6178) in anterior (**n**) and distal (**o**) views. Right fibula (MSM P6178) in proximal (**p**) and medial (**q**) views. Right tibia (MSM P6178) in proximal (**r**) and medial (**s**) views. **t**, Distal end of the tibia, fibula and the astragalus (MSM P6178) in anterior view. Left proximal halves of metatarsals II-IV (MSM P6178) in proximal (**u**) and anterior (**v**) views. **w**, Distal ends of metatarsals II-IV (MSM P4754) in anterior view. **x**, Pubic apron (MSM P6178) in anterior view. **y**, Partial manual ungual (MSM P6178) in lateral view. **z**, Partial left scapula (MSM P6178) in lateral view. Red color indicates elements preserved in the holotype (MSM P4754), blue color indicates elements preserved in the paratype (MSM P6178) and yellow color indicates elements preserved in both. Reconstruction copyright Scott Hartman. Abbreviations are as follows: 4^{th}, fourth trochanter; a., articulates with; as, astragalus; at, anterior trochanter; cc, cnemial crest; cr, cervical rib; fib, fibula; gl, glenoid; hs, histology sample location; hy, hyposphene; la, lacrimal; lc, lateral condyle; mt #, metatarsal number; or, orbit; pa, pubic apron; pf, pneumatic foramen; po, postorbital; stf, supratemporal fenestra; t, teeth; tib, tibia. Anterior arrow indicates anterior direction in H and Z. Scale bars = 1 cm. **[planned for 2 column width]**

Figure 3 | Histology section (in plain light) of the right femur (MSM P6178) of *Suskityrannus hazelae*, gen. et sp. nov. taken near the midshaft. a, complete section and **b**, closeup. Arrows indicate growth marks. Scales = 1 mm. **[planned for 1 column width]**

Figure 4 | The relationships of *Suskityrannus hazelae*, gen. et sp. nov. among

tyrannosauroids and its place within the transitionary Moreno Hill dinosaur assemblage. **a,** Phylogenetic position of *Suskityrannus hazelae*, gen. et sp. nov. as a 'mid-grade' tyrannosauroid found outside of Tyrannosauridae in all phylogenetic analyses presented here; and highlighting the acquisition of the arctometatarsalian condition in tyrannosauroids. Gray bars indicate stratigraphic uncertainty, not stratigraphic ranges. **b**, The Moreno Hill Assemblage is recovered during a time few dinosaur assemblages are known from Laurasia and sits in the critical transition prior to the diversification of tyrannosaurids, hardrosaurids, and ceratopsids (**c**) – all key components of classic latest Cretaceous dinosaur assemblages of North America (from[49]). **d**, The Moreno Hill dinosaur assemblage and its similar but better sampled Bissekty dinosaur (highly fragmentary forms not represented) assemblage represent the best dinosaur assemblages from the Turonian Stage in the northern hemisphere (see supplementary information).